

Research report

Common neural substrates for the control and effects of visual attention and perceptual bistability

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Abstract

Behavioral studies have suggested that bistable figure perception is mediated by spatial attention. We tested this hypothesis using event-related functional MRI. During central fixation, two tilted squares containing coherently moving dots were presented in the left and right hemifields. In the attention condition, participants were occasionally cued to shift attention between the squares. In the perception condition, corresponding corners of the squares were connected by horizontal lines producing a perceptually bistable Necker cube figure. Observers reported which of the two faces appeared 'forward' in depth; cues elicited voluntary perceptual reversals. Attending to either square during the attention condition or perceiving either square as forward during the perception condition yielded increased activity in contralateral visual areas. Furthermore, voluntary shifts of attention and voluntary shifts in perceptual configuration were associated with common activity in the posterior parietal cortex, part of the frontoparietal attentional control network. These results support the hypothesis that voluntary shifts in perceptual bistability are mediated by spatial attention.

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At the moment of first viewing, an object's identity is ambiguous, because any given retinal image is consistent with an infinite variety of possible scene configurations. Visual object recognition requires selection from among a vast number of viable matches stored in long-term memory. Typically, this ambiguity is resolved in a fraction of a second. Perceptually ambiguous (or bistable) figures such as the Necker cube [43] are a class of objects that support two or more stable visual interpretations that fluctuate over time [1].

Perceptual reversals of ambiguous figures have traditionally been attributed to cortical satiation [9,31,32,69], in which neural activity and subsequent fatigue elicit alternating perceptual configurations. More recently, top-down factors have been shown to play a critical role in ambiguous figure

perception: observers can voluntarily shift the perceptual configuration of ambiguous figures [46,47], an unambiguous prime can bias the interpretation of an ambiguous figure toward the corresponding perceptual configuration [37], and figures not known to be ambiguous often maintain their initial perceptual configuration [24,51]. A spatial attention hypothesis [47,70] has been proposed to account for these top-down effects, where shifts in the locus of spatial attention evoke a particular perceptual configuration.

In the present paper, we sought evidence from measurements of neural activity that the voluntary control of perceptual configuration in bistable stimuli is mediated by voluntary shifts of selective attention. This approach exploits the large body of existing evidence concerning the neural basis of visual attention (e.g., Refs. [11,29,74]).

Visual selective attention is a cognitive mechanism that permits behaviorally relevant stimuli to enter awareness. Two aspects of the deployment of attention in vision have

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been studied extensively using neurophysiological and neuroimaging techniques: the effects of attention on the magnitude of neural responses in early visual cortical regions, and the control of attention via feedback from executive control regions of the brain.

The effect of visuospatial attention to a stimulus at a peripheral location (while maintaining central fixation) is to increase the cortical response associated with that stimulus in striate and extrastriate visual areas within the contralateral hemisphere compared to when that stimulus is not attended (e.g., Refs. [8,25–27,39,59,75]). This contralateral attention effect has been shown to operate on the precise retinotopic cortical representation of the to-be-attended stimulus [4,40,60,61,68]. Visual attention can also operate by modulating the cortical responses to a given stimulus feature. For example, attention to motion increases activity in human motion processing region MT+ [12,35,45], the human homologue of monkey motion processing areas MT and MST [18,28].

By contrast, the control of spatial attention has been associated with activity in the dorsolateral prefrontal and posterior parietal cortex (e.g., Refs. [13,26,74]), with recent evidence indicating that transient activity within these regions serves as a signal to initiate a shift of attention between locations, features, or objects [35,52,72,75]. In short, the effect of attention is to modulate neural activity in visual areas, while the control of attention has been associated with transient activity in frontal and parietal cortex that is time-locked to attentional switches, in addition to sustained activity in these areas that maintains a given attentive state [14,15,27].

Studies of the control of ambiguous figure perceptual reversals have also revealed transient activity in the frontal and parietal cortex [30,38,63], suggesting that there may be a common mechanism subserving the voluntary deployment of attention and voluntary control over perceptual bistability. However, no studies have directly compared these two cognitive operations.

We hypothesized that spatial attention may mediate the perceptual configuration of ambiguous figures, both with regard to the maintenance of a particular perceptual configuration and with regard to shifts in perceptual configuration. The first aspect of the hypothesis was based upon previous behavioral work indicating attention toward a region within an ambiguous figure biases the perception of the corresponding configuration [47,70]. The second aspect of the hypothesis was based upon the similarity in the frontal and parietal regions associated with the control of attentional shifts [13,26,35,75] and shifts in ambiguous figure configuration [30,38,63].

To test this hypothesis, we used rapid event-related functional MRI (fMRI) to assess both sustained and transient effects associated with spatial attention and ambiguous figure perception. Fig. 1a illustrates the stimulus used in the attention condition. During central fixation, an auditory cue occurred every 14 s prompting participants to

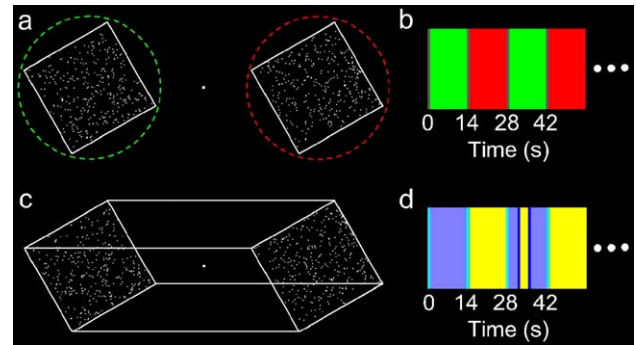


Fig. 1. Stimulus displays and experimental protocols used to compare spatial attention and ambiguous figure perception. (a) In the attention condition, participants fixated centrally while shifting attention between moving dots on the left (within the green dashed circle) and right (within the red dashed circle) according to the auditory cues “left” and “right” (circles were not present in the display). (b) Segment of attention condition behavioral protocol where attentional shifts are shown in dark grey, while sustained attention to the left and right are shown in green and red, respectively. (c) In the perception condition, the same auditory cues prompted voluntarily shifts in the perceptual configuration of the ambiguous figure, such that either the left or right face of the figure was perceived as ‘forward’ in depth. (d) Segment of perception condition behavioral protocol where voluntary shifts in perceptual configuration are shown in cyan, involuntary shifts in perceptual configuration are shown in dark blue, while sustained perception of the left face forward and right face forward are shown in light blue and yellow, respectively.

shift attention between the coherently moving dots in the left visual field and those in the right visual field (Fig. 1b, see Methods). Fig. 1c shows the stimulus used in the perception condition, an adaptation of the Necker cube.¹ In this condition, participants had been trained to shift the perceptual configuration of the ambiguous figure according to the same auditory cues such that its left or right face was perceived as ‘forward’ in depth (Fig. 1d).

A region-of-interest (ROI) approach was used to assess the sustained effects of attention and perception in early visual areas and region MT+, while a random effect approach was used to assess the control of attentional shifts and shifts in perceptual configuration. If our hypothesis is correct, and attention does mediate both the sustained and transient aspects of ambiguous figure perception, we expect similar patterns of activity in both visual areas and control regions.

1. Methods

1.1. Participants

Ten participants (5 females, aged 21–27 years) with normal or corrected-to-normal visual acuity were each paid US\$100 to take part in the study. The Johns Hopkins University institutional review board approved the exper-

¹ Strictly speaking, we used a “Necker rectangular parallelepiped”. The cube has been elongated in order to place the two faces in opposite visual hemifields. For convenience, we refer to it as a cube.

rimental protocol, and written informed consent was obtained from each participant before the experiment commenced.

1.2. Attention and perception tasks

The two main tasks were an attention task and a perception task, with nearly identical stimulus displays (Figs. 1a and c). During both tasks, participants were instructed to always maintain fixation at a central point. Both displays included two squares rotated 30° in polar angle from horizontal, with the nearest corners 2° of visual angle from fixation and an edge length 4° in visual angle. Within each square, 320 dots (each 0.05° in width) moved with a velocity of 5° of visual angle per second with a 40-ms frame rate and 70% coherence (see Ref. [44]). To avoid perceptual grouping, dots within the left square moved downward and dots within the right square moved upward. During both tasks, MR-compatible headphones were used to auditorily present the words “left”, “right”, “left”, “right”, and so on in alternation, every 14 s (cue words were never repeated twice in a row).

In the attention task, participants had been trained to interpret the auditory cue “left” to mean they were to shift spatial attention to the dots within the left square, and vice versa (Figs. 1a and b); participants continually held down the corresponding button in their dominant hand to indicate the current locus of attention. Every 2–12 s, dots on the attended side increased or decreased speed with equal probability for 250–400 ms. Participants pressed a response button in their non-dominant hand if the dots on the attended side speeded up (or slowed, depending on pre-run instructions). During a pre-scanning training session, the magnitude and duration of the dot velocity change in the attention task were calibrated to yield an accuracy of approximately 80% for each participant, such that the task required the maintenance of spatial attention at the to-be-attended location. This design yielded three types of cognitive events associated with the attention task: sustained attention to the left, sustained attention to the right, and attentional shifts (collapsed over shift direction).

In the perception task, participants were trained to report which face of the bistable figure was perceived as being forward in depth (Figs. 1c and d) by holding down the corresponding button in their dominant hand. They had learned that the auditory cue “left” indicated they should voluntarily reverse the perceptual configuration such that the left face of the cube was perceived as being in front, and vice versa for the auditory cue “right”. Participants were instructed to maintain the current perceptual configuration, if possible, making voluntary shifts in perceptual configuration only following a switch cue. Occasionally, however, involuntary shifts of perception occurred (with no immediately preceding switch cue); participants signaled this by an alternation of button press and had been instructed to maintain this new perceptual configuration. This aspect of

the design allowed us to isolate voluntary and involuntary shifts in perceptual configuration, allowing for a more appropriate comparison between voluntary attentional shifts in the attention task and voluntary shifts in perceptual configuration. Specifically, if a perceptual shift in configuration occurred, it was labeled voluntary if the appropriate cue had occurred at most 2 s before the button response, and was otherwise considered involuntary. Because involuntary shifts in perceptual configurations did occur, participants could also become ‘out of synch’ such that the cue word instructed the participant to ‘switch’ to the current perceptual configuration (e.g., the cue “left” when the left face was already perceived as forward in depth). In such cases, participants were instructed to maintain the current perceptual configuration—these events served as auditory controls (as they could be assumed to only be associated with auditory sensory stimulation and word processing, with no corresponding act of cognitive control to change the currently perceived configuration).

Every 2–12 s, one of the two horizontal bars nearest to fixation flashed red for 250–400 ms, matching the duration of the speed change in the attention task for each participant. Participants pressed a response button with their non-dominant hand if the bar was perceived in the ‘front’ of the figure (or in the ‘back’, depending on pre-run instructions). This task induced observers to attend to the bistable figure as a whole and to make judgments that depended on its currently perceived configuration. Although it is conceivable that participants might use a rule to make correct responses (e.g., “if I have been instructed to perceive the left face forward, then when the upper bar flashes, I should press the left key”), no participants reported doing so. Furthermore, if such a rule was used, null visual area effects would be expected; the positive findings reported below provide additional evidence that this did not occur. The design yielded five types of cognitive events associated with the perception task: sustained perception of the left face forward, sustained perception of the right face forward, voluntary shifts in perceptual configuration, involuntary (spontaneous) shifts in perceptual configuration, and auditory controls.

To determine whether participants were able to maintain fixation during the tasks, eye tracking was conducted outside the scanner on six of the participants using a SensoMotoric Instruments Eyelink System (Teltow, Germany).

1.3. Localizer tasks

For each participant, a bifield retinotopic mapping technique [58] similar to previously established methods [17,19,20,53,67] was used to identify borders between early visual areas (V1v, V1d, V2v, V2d, VP, V3, V4v, V3A). In addition, a human MT+ localizer was employed, consisting of a central fixation point surrounded by 400 randomly placed dots (each 0.05° across) within the rectangular visual display measuring $13.6^\circ \times 18.1^\circ$ of visual angle. In a

blocked design, the display alternated between stationary dots for 14 s and dots moving toward the fixation point for 14 s with 100% coherence and a velocity of 5° per second, supporting central fixation. At the beginning of every other motion period, participants heard the word “attend” and were instructed to press a response button when the dots briefly slowed (for 250 ms); “perceive” was heard at the beginning of the other motion periods, with no associated behavioral task.

1.4. MRI protocol

Data were acquired with a Philips ACS-NT 1.5-T scanner in the F.M. Kirby Research Center for Functional Brain Imaging at the Kennedy Krieger Institute, Baltimore. Functional images were acquired using T2-weighted echo planar imaging sequences. Imaging data in the attention, perception, and MT+ localizer tasks were collected with a Phillips end-capped quadrature birdcage head coil for whole-brain imaging with slices acquired axially (TR = 2 s, TE = 40 ms, flip angle = 90° , 26 slices, no gap, 4.5 mm isotropic resolution). For retinotopic mapping, a circular Phillips C3 surface coil centered under theinion was used for occipital imaging with slices acquired in the coronal-oblique orientation (TR = 3 s, TE = 40 ms, flip angle = 90° , 20–30 slices, no gap, 3 mm isotropic resolution). Anatomic images were acquired using a T1-weighted MPRAGE sequence (TR = 8.1 ms, TE = 3.7 ms, flip angle = 8° , 1 mm isotropic resolution). During scanning, all participants completed 2 attention runs and 4 perception runs, each lasting 154 timepoints (308 s), and at least 1 retinotopic mapping and MT+ localizer run, each lasting 117 and 224 timepoints (351 and 448 s), respectively.

1.5. fMRI analysis

All data analysis was conducted using BrainVoyager (Brain Innovation, Maastricht, The Netherlands). Pre-processing included slice-time correction, motion correction, and temporal high-pass filtering above 3 cycles per run length (spatial filtering was not used). For each participant, the anatomic and functional volumes were then transformed into Talairach space [64]. Anatomic hemispheres were segmented at the grey/white matter boundary, and the surface was reconstructed, inflated, cut at the fundus of the calcarine sulcus, flattened, and distortion corrected to less than 15% linear distortion [60,61] using methods similar to others [16,53,67,71].

Data were analyzed separately to assess sustained visual area effects and transient whole-brain effects. In our event-related analyses, the hemodynamic response associated with each event type was first modeled by convolving its associated protocol-defined by temporal onsets and durations—with a gamma function (see Refs. [3,10,42]), and then these model time series were entered into a general linear model that was fit to each voxel’s activation

timecourse. This yielded a beta weight associated with each event type. Statistical contrasts between beta weights were used to identify voxels with differential event-related activity.

1.5.1. Sustained activity in visual areas

As sustained visual attention effects are known to occur within visual cortical regions, an ROI analysis was conducted to assess both sustained attention and perception effects, restricted to early visual areas (V1v, V1d, V2v, V2d, VP, V3, V4v, V3A) and MT+ on the flattened cortical surface representation of each participant. The borders between early visual regions were obtained using retinotopic mapping procedures on an individual participant basis (because the border locations vary between participants). An event-related correlation analysis was conducted (with $r > 0.25$), where each of the angular positions of the rotating and flickering checkerboard stimulus wedges was associated with a particular phase (or color in the resulting cortical flat map), and reversals in phase demarcate borders between visual areas (for full details, see Ref. [58]).

In addition, the approximate border surrounding MT+ was localized for each participant (in both the right and left hemispheres) by contrasting attention to moving dots versus perception of stationary dots, constraining the resulting activation to the known anatomical locus of MT+ near the ascending limb of the inferior temporal sulcus [73]. This contrast was used to maximize the size of the effect in MT+, as attention to motion has been shown to increase activity in this region [12,35,45]. In this and subsequent visual area-related statistical tests, individual voxel thresholds were set to $P < 0.05$ with a cluster extent threshold of 820 mm^3 (135 mm^2 on the 2-dimensional cortical surface), thus correcting for multiple comparisons to $P < 0.01$ [21,56,60,61]. We deliberately selected a relatively relaxed individual voxel threshold in the visual area analysis (as compared to the whole brain analysis; see below) because here the activity served to identify specific functional ROIs, within which event-related timecourses were extracted to make statistical inferences.

The sustained event types (sustained attention to the left, sustained attention to the right, sustained perception of the left face forward, and sustained perception of the right face forward) were all entered into a general linear model. Event durations were defined behaviorally, as measured from the beginning to the end of each button press (which reflected sustained attention to the corresponding side or perceptual configuration of the corresponding side forward). The contrast between attention to the right and attention to the left, and vice versa, was used to identify standard contralateral attention effects. The contrast between perception of the left face forward and perception of the right face forward, and vice versa, was expected to elicit corresponding contralateral effects (if the hypothesis that attention mediates bistable perception is correct). The neural locus of the activity associated with these contrasts

was identified with reference to early visual area and MT+ borders on the flattened representation of the occipital cortex.

Event-related activation timecourses—a plot of the mean activity associated with each event type as a function of time, time-locked to event onset—were extracted from cortical ROIs (with surface area 25 mm²). The baseline of each timecourse (i.e., 0% signal change) was defined as the level of activity from 2 to 0 s preceding stimulus onset, and linear trends were removed by fitting a line to the timecourse from –2 to 20 s and then removing that linear component (to eliminate local linear trends within that epoch that were not removed with high pass filtering). To avoid violating the assumption of data independence (had we averaged across timepoints), statistical assessment was restricted to the timecourse magnitude 6 s following cue onset, a value determined a priori as it was expected to reflect the maximal response given the known hemodynamic response lag [14,33,60,61]. These values were entered into a within hemisphere two-factor ANOVA to assess the main effects and interaction of condition (perception and attention) and visual area (V1v, V1d, V2v, V2d, VP, V3, V4v, V3A, and MT+) across hemispheres. Paired *t* tests were used to assess the effects of each condition within a given visual area, and one-tailed *t* tests were used to directly contrast these effects.

1.5.2. Transient activity

A random effect analysis [23,22] was conducted to assess transient attention and perception effects across all participants. First, an individual participant whole brain general linear model analysis was conducted to estimate the beta weight associated with all four transient event types (attentional shifts, voluntary shifts in perceptual configuration, involuntary shifts in perceptual configuration, and auditory controls). Second, for a given contrast of interest, only voxels associated with a beta weight difference that was statistically consistent across participants were deemed active (i.e., between participant variability was used to estimate variance). For this analysis, voxel thresholds were set to $P < 0.01$. Furthermore, a cluster extent threshold of 287 mm³ was enforced to correct for multiple comparisons to $P < 0.01$ [21,56,57,60,61].

To better isolate regions associated with voluntary shifts in attention and voluntary shifts in perceptual configuration (from auditory processing), these event types were contrasted with auditory control events. The offset times associated with shifts in attention and perceptual configuration were time-locked to the button response associated with shifts, with the onset times for both events being defined as occurring 1 s earlier. Auditory control event onsets were time-locked to the cue word and were also modeled with a 1-s duration. It should be noted that shifts in attention and perceptual

configuration were both confounded with a button response; fortunately, activity due to motor processing can be easily identified [48] and thus separated from the attention- and perception-related results that are of interest. Furthermore, to identify the cortical regions that were associated with both shifts in attention and perceptual configuration, we performed a conjunction analysis with the two contrast pairs (i.e., shifts in attention versus auditory controls and shifts in perceptual configuration versus auditory controls) were participated to a conjunction analysis [6,22,23], still enforcing voxel and corrected for multiple comparison P values < 0.01 . Finally, shifts in attention were directly contrasted with shifts in perceptual configuration, and vice versa, to identify the regions differentially involved in these cognitive functions. Significant activity associated with the conjunction and two contrasts was projected onto the surface reconstruction of one representative participant. It is important to consider that this participant's neuro-anatomical configuration is necessarily different than that of the group average; therefore, the activity pattern projected on the participant's cortical surface should only be considered a reflection of the group results.

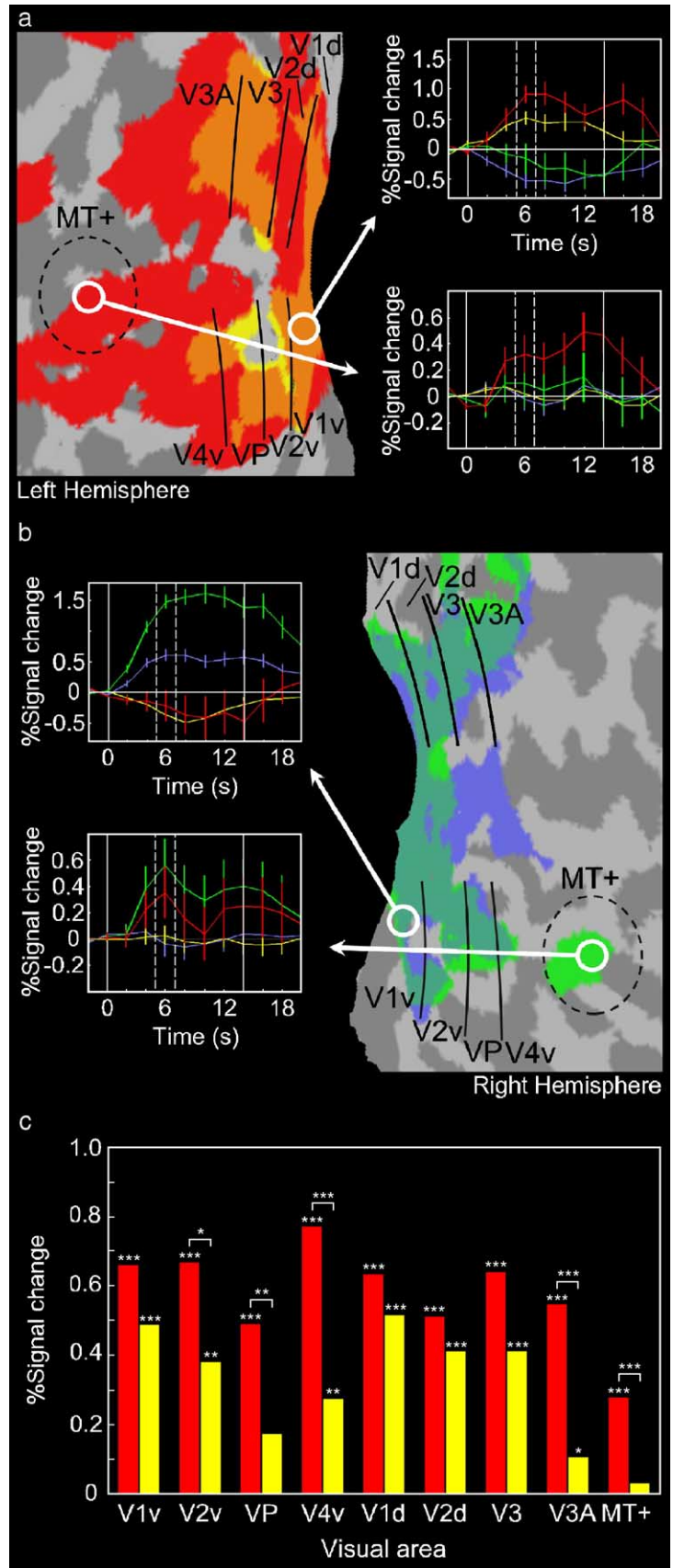
2. Results

2.1. Behavioral results

Target identification accuracy during the attention task (detecting changes in dot speed) was $84.1 \pm 2.1\%$ (mean \pm one standard error), and accuracy during the perception tasks (detecting bar flash) was $83.3 \pm 2.8\%$. The similar accuracy rates suggest that task difficulty was well matched between conditions (paired $t < 1$, $P = 0.86$). All six participants tested outside of the MRI scanner maintained fixation to within 0.5° of the central fixation point during the tasks.

2.2. Sustained activity in visual areas

Fig. 2a (to the left) illustrates the effects of shifting attention and perception in the left hemisphere of one participant, including regions with greater sustained activity associated with attention to the right versus attention to the left (in red), and perception of the right face forward versus perception of the left face forward (in yellow, with overlap in orange). The observation that cortical activity increases contralateral to the locus of spatial attention replicates a widely reported pattern (e.g., Refs. [4,8,25–27,39,40,59,60,61,68,75]). These individual hemisphere results (see Fig. 2b, to the right) are representative of all participants and illustrate the large degree of overlap between attention and perception effects across early visual areas (V1v, V1d, V2v, V2d, VP, V3, VP, V4v, V3A).



The spatial extent of the perception effects within early visual areas was generally more restricted than that of the attention effects. Furthermore, perception effects were completely absent within MT+. The event-related activity timecourses extracted from V1v in the left hemisphere of this participant (Fig. 2a, upper right; also representative of other regions that were commonly active) confirmed the contralateral and sustained nature of the attention effects (red > green) and perception effects (yellow > light blue), while event-related timecourses from MT+ (Fig. 2a, lower right) exhibited only attention effects. A complementary pattern was observed in the right hemisphere of the same participant (Fig. 2b).

Fig. 2c depicts the magnitude of the attention and perception effects within each visual area across all hemispheres ($n = 20$). A significant main effect of condition ($F(1,19) = 21.94$, $MS_{\text{error}} = 0.29$, $P < 0.001$) indicated that the magnitudes of the attention effects were greater overall than those of the perception effects. The significant main effect of visual area ($F(8,152) = 4.28$, $MS_{\text{error}} = 0.19$, $P < 0.001$) indicated that the magnitude of both effects differed across visual areas, and the interaction between condition and visual area ($F(8,152) = 2.67$, $MS_{\text{error}} = 0.07$, $P < 0.01$) indicated that relative sizes of the attention and perception effects differed across visual areas. There were significant attention effects in all areas and significant perception effects in all areas except VP and MT+. Although motion processing is typically associated with activity in MT+, VP has also been associated with more complex motion processing [54,62,66] and was probably driven by the coherently moving dots. A direct contrast between the magnitude of attention and perception effects within each visual area revealed greater attention effects in visual areas V2v, VP, V4v, V3A, and MT+. The differential sustained effects of attention and perception in VP and MT+ can be attributed to attention-related enhancement of motion processing [12,35,45].

2.3. Transient activity

Several regions were associated with both shifts of attention and shifts of perceptual configuration, relative to the auditory control (Fig. 3 and Table 1). The superior parietal lobule and intraparietal sulcus exhibited transient increases in activity time locked to the initiation of voluntary shifts of attention; this finding replicates previous findings that have associated posterior parietal regions with shifts of attention (e.g., Refs. [3,26,35,52,72,75]). These same regions were associated with shifts of perceptual configuration. Transient increases in activity were also observed in sensorimotor regions associated with the button response, including the pre-central gyrus (primary motor cortex), the post-central gyrus (sensory cortex), the medial frontal gyrus (supplementary motor area), and the cingulate sulcus (cingulate motor area) [48]. In addition, the supra-marginal gyrus activity observed here has also been associated with auditory processing [7,55] and may represent enhanced word processing during the main tasks as compared to the control task. We also observed transient activity associated with shifts in attention and shifts in perceptual configuration within the extrastriate cortex, most extensively in ventral temporal visual areas. Event-related timecourses were extracted from the region of activity within the right superior parietal lobule (Fig. 3, upper middle) to illustrate the transient activation profiles associated with shifts in attention and shifts in perceptual configuration. The same pattern of event-related activity was observed in all commonly active regions.

The contrast between transient shifts in attention greater than shifts in perceptual configuration revealed no significant regions of activity, while the reverse contrast between shifts in perceptual configuration greater than shifts in attention was associated only with activity within the anterior cingulate gyrus (Fig. 3, bottom right). Event-related timecourses were extracted from this region (Fig. 3, lower middle) and revealed transient increases in activity asso-

Fig. 2. Sustained early visual area attention and perception effects. (a) To the left, flattened left hemisphere surface reconstruction of a representative participant, where gyri and sulci are colored light and dark grey, respectively. Before flattening, a cut was placed at the fundus of the calcarine sulcus, which runs along the rightmost edge in this depiction. The black lines demarcate early visual area borders, and the dashed black ellipse defines the boundary of human motion processing complex MT+. Dorsal and ventral visual areas are toward the top and the bottom, respectively. Cortical regions in which sustained attention to the right elicited significantly greater activity than sustained attention to the left (i.e., contralateral attention effects) are shown in red. Cortical regions in which sustained perception of the right face forward elicited significantly greater activity than sustained perception of the left face forward are shown in yellow. Orange regions represent the overlap of sustained attention and sustained perception effects. White circles represent ROIs used to extract event-related activity timecourses (relative to baseline activity from 2 to 0 s before event onset). The V1v ROI event-related activity timecourses are shown to the upper right. Red and green timecourses correspond to sustained attention to the right and left, respectively, while yellow and light blue timecourses correspond to sustained perception of the right and left face forward, respectively (\pm one standard error of the mean reported). Dotted lines flank the 6 s timepoint, which was used to statistically evaluate the attention and perception effects, defined as the difference in magnitude between attention-related effects (red minus green) and perception-related effects (yellow minus blue). The MT+ ROI event-related activity timecourses are shown to the lower right. (b) To the right, flattened right hemisphere surface reconstruction of the same participant (the calcarine sulcus is along the leftmost edge), with visual area borders and boundaries of MT+ demarcated in black. Regions in which sustained attention to the left elicited significantly greater activity than sustained attention to the right are shown in green, while regions in which sustained perception of the left face forward elicited significantly greater activity than sustained perception to the right face forward are shown in light blue. Turquoise regions represent the overlap of sustained attention and sustained perception effects. Event-related timecourses from the V1v and MT+ ROIs are shown to the left (using the same color scheme described above). In this hemisphere (as compared to the left hemisphere), the opposite comparison was used to compute attention-related effects (green minus red) and perception-related effects (blue minus yellow). (c) Across participants, mean attention (red) and perception (yellow) effects in early visual areas and MT+. Within each region, the significance of each effect in addition to the contrast between effects was computed $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

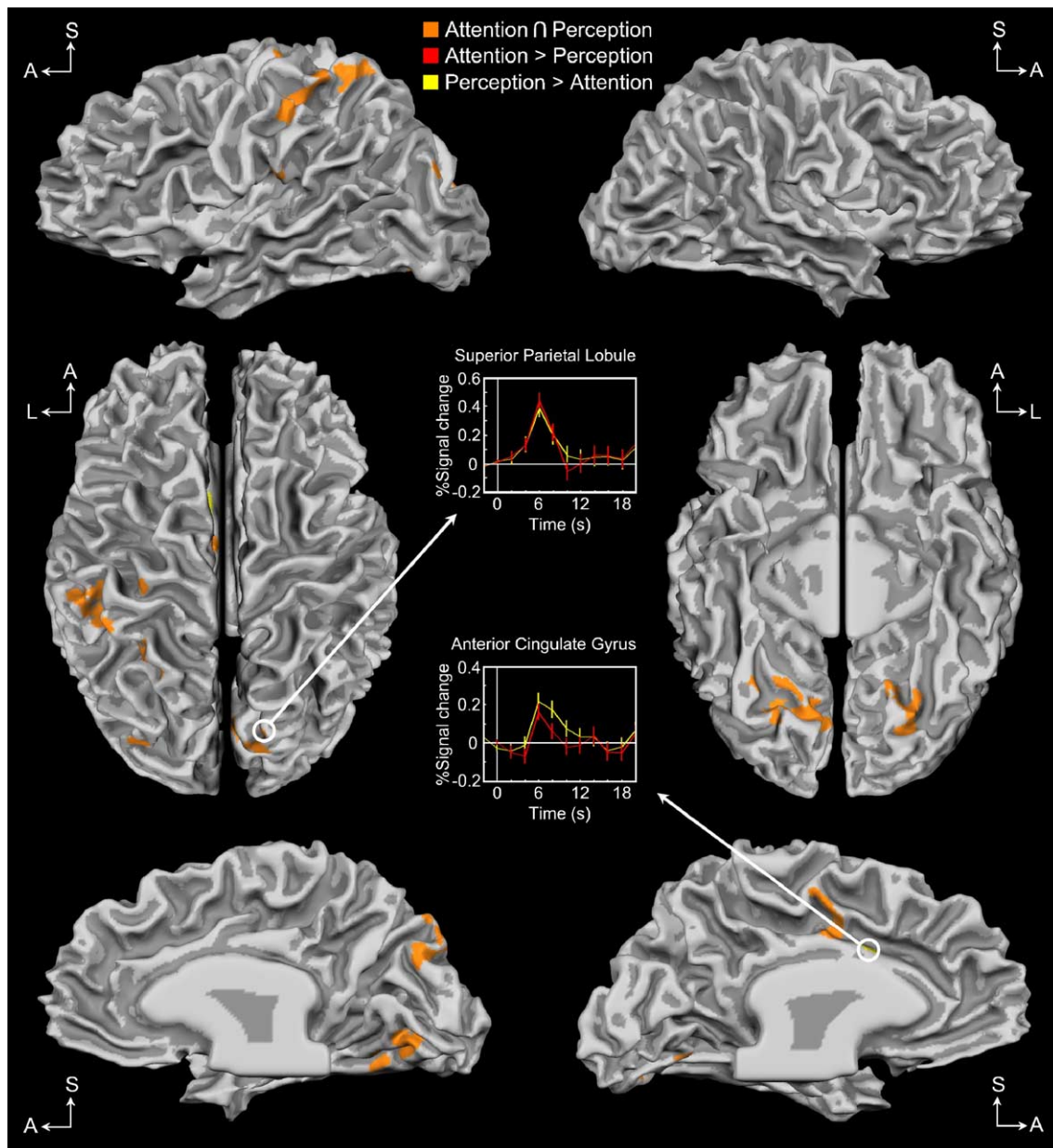


Fig. 3. Transient whole-brain attention and perception group effects (projected onto a representative participant's cortical surface). Multiple views of the reconstructed cortical surface are shown, where gyri and sulci are colored light and dark grey, respectively. Lateral views of the left and right hemisphere are toward the upper left and upper right, respectively (A refers to anterior; S refers to superior). Superior and inferior views of both hemispheres are toward the middle left and middle right, respectively (L refers to left). Medial views of the right and left hemisphere are toward the lower left and lower right, respectively. Regions associated with both attentional shifts and shifts in perceptual configuration are shown in orange (see Table 1), and regions differentially associated with attentional shifts and shifts in perceptual configuration are shown in red and yellow, respectively (see key at top center). Event-related activity timecourses were extracted from a superior parietal lobule ROI (with similar activity profiles) and an anterior cingulate gyrus ROI (with differential activity profiles), as illustrated in the upper and lower middle, respectively.

ciated with both event types, relative to the baseline level of activity (confirmed via post hoc paired t tests; $t_{\text{attention}}(9) = 10.07$, $P < 0.001$; $t_{\text{perception}}(9) = 12.62$, $P < 0.001$), and significantly greater activity associated with shifts in perceptual configuration at 8 s following stimulus onset, with a marginally significant effect at 10 s (as assessed with post hoc paired t tests; $t_{8\text{ s}}(9) = 2.65$, $P < 0.05$; $t_{10\text{ s}}(9) = 2.18$, $P < 0.10$).

3. Discussion

We observed sustained increases in activity contralateral to the locus of voluntary spatial attention, corroborating many previous reports of contralateral attention effects in early visual areas (e.g., Refs. [4,8,25–27,39,40,59,60,61,68,75]). These same regions exhibited increased contralateral activity when observers voluntarily perceived

Table 1
Regions commonly and differentially associated with shifts of attention and perception

Region	BA	(x, y, z)	Z score
Attention \cap Perception			
Right superior parietal lobule	7	11, -76, 42	2.96
Left superior parietal lobule	7	-22, -53, 57	3.89
Left intraparietal sulcus	40	-38, -29, 42	3.26
Left medial frontal gyrus	6	-1, -8, 48	3.94
Left cingulate sulcus	6/24	-5, -5, 35	3.47
Left precentral gyrus	4	-39, -16, 54	2.92
Left postcentral gyrus	2	-52, -26, 40	3.17
Right supramarginal gyrus	40	51, -22, 19	3.74
Left supramarginal gyrus	40	-56, -23, 18	3.54
Left lateral occipital gyrus	19	-27, -80, 30	3.57
Right fusiform gyrus	19	30, -60, -11	2.97
Left fusiform gyrus	19	-25, -73, -13	2.73
Right lingual gyrus	19	15, -57, -11	3.25
Left lingual gyrus	19	-17, -59, -7	2.93
Right cuneus	18	7, -74, 26	3.84
Right lingual gyrus	18	9, -67, -4	3.16
Attention > Perception			
No regions	-	-	-
Perception > Attention			
Left anterior cingulate gyrus	24	-1, 10, 33	4.29

BA refers to Brodmann area and coordinates (x, y, x) are reported in Talairach space. Z score refers to the most statistically significant voxel within a region. Symbols \cap and $>$ represent beta weight conjunction and contrast, respectively.

the ambiguous Necker cube figure with the left or right face forward (Fig. 2). The fact that perception-related activity generally had a smaller spatial extent than the attention-related activity suggests there were some difference between these cognitive operations. For instance, it may have been the case that the attention condition was associated with sustained attention to the cued location, while the perception condition was initially associated with attention to the cued location but later attention may have shifted to a more balanced position due to the requirement to perceive the object as a whole. Still, that the sustained differences in contralateral cortical activity were largely the same for attention and perception tasks suggests that the deployment of visual attention mediates the sustained perceptual configuration of ambiguous figures. The present results can also be taken as evidence against the cortical satiation hypothesis of bistable figure perception, which assumes alternating perceptual configurations are due to the neural activity and subsequent fatigue associated with the representation of the entire object [9,31,32,69]. Specifically, cortical satiation would not predict the observed contralateral perception effects (which instead support the visual attention hypothesis).

Voluntary shifts in attention and perceptual configuration were also both associated with transient increases in activity within the superior parietal lobule and intraparietal sulcus, which corresponds well with previously reported frontoparietal activity associated with both of these cognitive processes [13,26,30,35,38,63,72,75]. The tempo-

ral resolution of the BOLD fMRI signal is too coarse to determine directly whether these transient signals preceded the shifts in sustained activity within extrastriate regions. However, given the extensive body of evidence that this transient activity reflects the initiation of voluntary control, we tentatively conclude that it preceded or triggered the sustained effects described above.

In addition to the sustained and transient cortical activity that was evoked by shifts in both attention and perceptual configuration, some other findings emerged. First, we observed standard sensorimotor response patterns associated with button responses. Second, we observed feature-specific attentional modulation in motion selective areas VP and MT+ [54,62,66], corroborating previous reports [12,35,45]. These areas did not respond differentially to the two perceptual configurations, which may at first seem counter-intuitive. However, the perception condition required attention to the configuration or structure of the stimulus, rather than to the moving dots. As such, little if any attention-related increase in motion processing would be expected during the perception condition, explaining the non-significant effects within VP and MT+.

Finally, we observed transient activity in extrastriate visual areas. Two possible accounts for this unexpected extrastriate activity can be considered. One is that these extrastriate areas are part of the cognitive control circuit that initiates shifts of attention and perception. This possibility is unlikely, however, given the large body of evidence implicating posterior parietal and dorsolateral prefrontal cortex in the control of visual attention. A second, more plausible interpretation is that it may reflect a transient increase in visual processing associated with stimulus processing onset (as evoked during an attentional shift or perceptual reversal). A similar pattern of activity has been observed during object-based shifts of attention [52]. If this interpretation is correct, it provides further evidence for the common neural basis of voluntary shifts of attention and perceptual configuration.

Although we found no region that exhibited greater transient activity associated with attention shifts than with shifts of perceptual configuration (suggesting again a similar neural basis for these two cognitive functions), we did observe greater activity for perceptual shifts than for attention shifts in the anterior cingulate cortex. Subsequent testing within this region revealed increases in activity associated with both shifts of attention and shifts of perceptual configuration, but with relatively more sustained activity associated with shifts in perceptual configuration. This sustained anterior cingulate activity may be the result of relatively greater conflict [2] between alternate perceptual configurations. This does not undermine, however, the conclusion that the pattern of transient cortical activity associated with attentional shifts is almost identical to that associated with shifts in perceptual configuration.

We take the finding of similar sustained activity patterns in visual sensory areas and similar transient activity

patterns in posterior parietal and other attentional control areas to show that attentional shifts and perceptual configuration of ambiguous stimuli are mediated by common neural substrates. This provides converging evidence for the hypothesis that visual spatial attention mediates ambiguous figure perception. The present neuroimaging evidence compliments and extends previous behavioral work that has suggested a spatial attention account of sustained ambiguous figure perception [47,70].

Although observers occasionally “lost” the currently intended interpretation of the cube (following spontaneous perceptual shifts), they did not spontaneously shift attention. This suggests that attention is not the sole determinant of perceptual shifts. Perceptual fatigue probably does play a role in at least some perceptual reversals. However, this does not undermine our main conclusion that visual selective attention plays a central role in mediating voluntary shifts of perception.

The present findings may also have implications for other forms of perceptual bistability. In binocular rivalry, for example, different stimuli are presented to each eye and visual experience alternates between one stimulus and the other. Cortical activity increases in regions associated with processing a particular stimulus type when that stimulus dominates conscious awareness [34,65]. The stimuli employed during binocular rivalry have been shown to fall under the category of ambiguous figures [36], and the alternation rate of binocular rivalry is under voluntary control, albeit to a substantially lesser degree than bistable perceptual figures [41]. The present results suggest that shifts in perceptual configuration during binocular rivalry may be driven to some degree by shifts of attention between the rivalrous stimuli.

Another example of perceptual ambiguity is amodal completion, in which the visual system reconstructs the complete structure of a partly occluded surface. Recent evidence suggests that amodal completion yields both a fragmented representation and a complete representation, one of which dominates conscious awareness, depending on context and other factors [5,49,50]. The present results suggest that the deployment of attention to one of these interpretations might bias its perceptual representation and contribute to ambiguity resolution. Future work will be required to clarify the generality of attentional influences in the perceptual organization of ambiguous stimuli.

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